21. The External Characters and Classification of the Procyonidæ. By R. I. Pocock, F.R.S.

[Received February 5, 1921 : Read April 19, 1921.]

(Text-figures 1–13.)

Contents.

Introduction.

To show the wide divergence of opinion on the classification of the genera assigned in the current text-books to the Procyonidæ, it is needless to go to an earlier date than 1869, when Gray published his 'Catalogue of Carnivorous . . . Animals.' Using in the main the carnassial teeth, this author divided the Feræ into two suborders, Carnivora and Omnivora, the latter, with the teeth in question non-sectorial, comprising the forms now relegated as a rule to the families Ursidæ and Procyonidæ. Gray, however, admitted six families of Omnivora:—(1) Ursidæ with several genera; (2) Nasuidæ for *Nasua*; (3) Procyonidæ for *Procyon* with two subgenera *Procyon* and *Euprocyon*; (4) Cercoleptidæ for *Cercoleptes* (*Potos*); (5) Bassaridæ for *Bassaris*; (6) Ailuridæ for *Ailurus*.

In the same year, however, Flower (P. Z. S. 1869, pp. 4–37) classified the genera in question into the three families Procyonidæ (*Procyon*, *Bassaris*, *Nasua*, *Cercoleptes*); Ailuridæ (*Ailurus*); and Ursidæ (*Ursus*) *.

In 1872, Gill, whose estimate of the value of characters was far in advance of his time, made a classification which may be described as a combination of Gray's and Flower's (Smiths. Misc. Coll. xi. pp. 58–59, 66–67, 1872). It was as follows:—Fam. Ursidæ (with the genera admitted by Gray); Fam. Æluridæ (*Ælurus*); Fam. Cercoleptidæ (*Cercoleptes*=*Potos*); Fam. Procyonidæ with the subfamilies Nasuinæ (*Nasua*), Procyoninæ (*Procyon*); Fam. Bassaridídæ (*Bassaris*).

* This grouping, however, was the same in substance as that proposed by Turner about twenty years earlier (P. Z. S. 1848, p. 86) with the conversion of Turner's subfamilies Ursina, Ailurina, and Procyonina of the family Ursidæ into families of the Arctoidea.

In 1876 (Proc. Acad. Nat. Sci. Philad. pp. 20–23), J. A. Allen described the genus *Bassaricyon* and remarked: "As the species [*B. gabbi*] differs more from either *Nasua* or *Procyon* than the latter do from each other, it seems to form a type quite as well entitled to rank as a subfamily of the Procyonidæ as do either of the others, and may hence be called Bassaricyoninæ."

In 1883 (Encycl. Brit. (9) xv. p. 441), Flower repeated his classification of 1869 with the addition of *Bassaricyon* to the Procyonidæ and of *Ailuropus* to the Ursidæ.

In 1885, Mivart (P. Z. S. 1885, pp. 392–394) adopted Flower's views, with one or two important exceptions. He admitted only two families, the Ursidæ and Procyonidæ, fusing the Ailuridæ with the latter and relegating *Ailuropus* to a place alongside *Ailurus*. His Procyonidæ, therefore, were grouped as follows:—(1) Procyoninæ (*Procyon*, *Nasua*, *Bassaris*, *Bassaricyon*, *Cercoleptes*); (2) Ailurinæ (*Ailurus*, *Ailuropus*). It may be noted that after comparing the dental and cranial characters of *Ailurus* and *Ailuropus*, he summed up by saying ". . . . so that on the whole it appears to me that there is more decided natural affinity between *Ailuropus* and *Ailurus* than between *Ailuropus* and *Ursus*."

Mivart was, I believe, the first author definitely to assign *Ailurus* and *Ailuropus* to the Procyonidæ. Nevertheless, when Flower and Lydekker published their volume on the Mammalia in 1891, they quoted Blanford as the authority for the opinion they adopted that *Ailurus* belongs to that family. *Ailuropus* they retained in the Ursidæ.

Similarly, in their paper upon *Æluropus*, published in 1901 (Tr. Linn. Soc., Zool. viii. pp. 161–173), Lankester and Lydekker do not appear to have consulted Mivart's paper or to have been acquainted with his views; and the result was that Lydekker put forward a classification of the Procyonidæ identical in every particular with that of Mivart.

Trouessart (Cat. Mamm. Suppl. pp. 183–184, 1904) referred *Ailuropus* and *Ailurus* to the Ursidæ, grouping them in the subfamily Ailurinæ as opposed to the Ursinæ containing the genera of true bears. The Procyonidæ he divided into two subfamilies, the Potosinæ for *Potos* (olim *Cercoleptes*) and the Procyoninæ for *Bassaricyon*, *Bassariscus*, *Nasua*, and *Procyon*. With the substitution of Potosinæ for Cercoleptinæ, this classification is the same as that published by Trouessart in 1898 (Cat. Mamm. i. p. 248).

In 1914, Bardenfleth (Mindeskrift, etc., for J. Steenstrup's Födsel, Copenhagen, no. xvii. pp. 1–15) reconsidered the question of the affinities of *Ailurus* and *Ailuropoda*, and, deciding that the resemblances between them are purely adaptive, left the former in the Procyonidæ and adopted Flower's view that *Ailuropoda* is an aberrant member of the Ursidæ. The author tabulates in three columns, devoted respectively to *Ailurus*, *Ailuropoda*, and *Ursus*, no fewer than 58 characters by which these genera may

be compared and contrasted, the only character quite inadequately dealt with being the feet, wherein he would have found considerable corroborative evidence supporting his opinion of the Ursine affinities of *Ailuropoda*.

The latest classification was published in 1916 by Hollister (Proc. U.S. Nat. Mus. 49, pp. 141–150), who, following Gray and Gill, separated *Bassariscus* from the rest of the genera, his grouping being as follows:—Fam. 1. Bassariscidæ (*Bassariscus*); Fam. 2. Procyonidæ (*Ailurus*, *Procyon*, *Nasua*, *Nasuella* *, *Bassaricyon*, *Potos*). This grouping involves the conclusion that the affinity between *Ailurus* and *Procyon* or *Potos* is greater than the affinity between *Procyon* or *Potos* and *Bassariscus*, a conclusion which, in my opinion, is quite indefensible. With regard also to the affinities of *Potos* and *Bassariscus* with the other genera, I cannot agree with Hollister, whose opinion with regard to the dentition of *Bassariscus* may be contrasted with that of Flower when he wrote in 1869 "*Cercoleptes* [*Potos*] deviates in its dentition from the more typical members of the group far more than *Bassaris* [*Bassariscus*], though in a precisely opposite direction."

From the above-given review it will be evident that there is no sort of unanimity on the three following points:—(1) The position of *Ailuropoda* †. Some authors claim that the genus belongs to the Ursidæ; others place it in the Procyonidæ. (2) The position of *Ailurus* ‡, some authors regarding it as the type of a special family, others, in a majority, placing it in the Procyonidæ. (3) The constitution of the so-called Procyonidæ of America. Every genus has at various times been made the representative of a special family or subfamily. Justification for this course is to be found in the much greater differences that exist between them than between the genera of Felidæ, Canidæ, and other compact families of Carnivora.

This variety of opinions calls for a revision of the questions at issue in the light of other characters than those supplied by the teeth, skull, and skeleton, which have mainly been used. Gray, it is true, employed the feet to a certain extent, but he was compelled to depend very largely upon dried skins, and most authors attach comparatively slight importance to external characters.

During the past few years I have been making sketches of the feet, ears, rhinaria, and other external organs of the Carnivora that have died in the Gardens of the Zoological Society: and the

* To illustrate the differences between *Nasua* and *Nasuella* and justify the creation of the latter, Hollister seems to have selected skulls exhibiting extremes of variation. I have skulls of *Nasua* almost intermediate between the two figures.

† This was the name originally given to the genus by Milne Edwards; but he subsequently changed it to *Ailuropus* because Gray had previously employed the name Æluropoda for a section of the Carnivora comprising the Felidæ, Mustelidæ, and other families. Gray's action, however, did not invalidate the use of *Ailuropoda* in a generic sense. I have, therefore, retained it.

‡ The original spelling of this name is also adhered to in this paper.

present paper is based mainly upon the Procyonidæ examined in the Prosectorium.

The following material has passed through my hands:—

Ailurus fulgens.—Several specimens of both sexes.

Procyon lotor or closely-allied forms.—Several specimens of both sexes.

Nasua nasua (ring-tailed Coati Mondi, with a dark snout and distinctly ringed tail).—Several specimens.

Nasua narica (the white-nosed Coati Mondi, with a white snout and indistinctly ringed tail).—Several specimens.

Bassaricyon sp.—A single specimen, sent on approval by Mr. Cross, the animal dealer, which died on the day of its arrival and had to be returned to the vendor. Of this only the feet and rhinarium were sketched. My observations on this genus have been supplemented by an examination of the dried skins in the British Museum.

The example of this genus dissected by Mr. Beddard (Proc. Zool. Soc. 1900, pp. 661–675) was converted into a skeleton.

Potos caudivolvulus or closely-allied forms.—Several specimens of both sexes.

Bassariscus astutus.—A single immature male preserved in alcohol—probably the specimen whose anatomy was described by Mr. Beddard (Proc. Zool. Soc. 1898, pp. 129–131).

Jentinkia sumichrasti.*—Dried skins in the Natural History Museum. This Cacomistle is sometimes admitted as a subgenus of *Bassariscus*. I have provisionally quoted it as a distinct genus, the material available being insufficient to establish the absolute constancy of the differences in the feet observable between *astutus* and *sumichrasti*.

Ailuropoda melanoleuca.—Mounted specimen and skull in the Natural History Museum.

The skulls examined are in the collection of the Zoological Society and in the Natural History Museum.

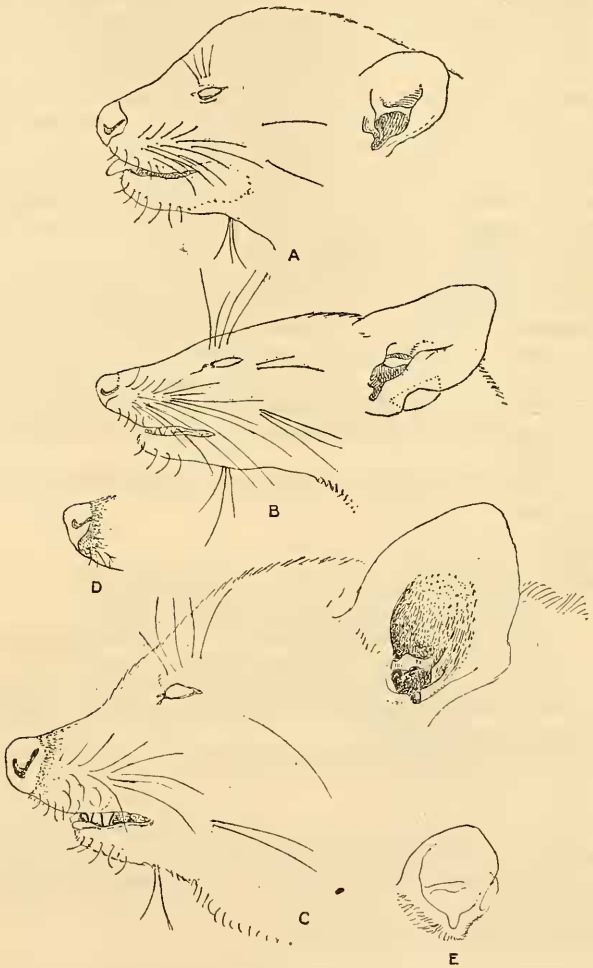
The External Ear.

As recorded by previous authors, the pinna of the ear varies in shape and size, being short and rounded in *Nasua*, *Potos*, and *Bassaricyon*, longer, more pointed, and more expanded in *Procyon*, *Bassariscus*, *Jentinkia*, and *Ailurus*. The cartilages strengthening the base of the ear are simple and normally carnivorous in their arrangement, requiring no special description, especially as they vary in development to a certain extent

* Proposed by Trouessart (Cat. Mamm. Suppl. p. 184, 1904) to replace the preoccupied name *Wagneria* Jentink (Notes Leyd. Mus. viii. p. 129, 1886) based on the differences between *B. variabilis* [*sumichrasti*] and *astutus* pointed out by Peters (Mon. Ak. Wiss. Berlin, 1874, pp. 704–705).

within generic limits. Much greater interest attaches to the *bursa*. In *Bassariscus* and *Jentinkia* this is developed as in the Canidæ, Felidæ, and some Viverridæ, its posterior half being formed by

Text-figure 1.



A. Head of *Potos caudivolvulus* (vel *sp. aff.*). ♂ ad. × ½.
B. „ *Bassariscus astutus*. ♂ immat. × ½. (From specimen in spirit with ear half closed and hair wet.)
C. „ *Procyon lotor*. ♂ ad. × ½.
D. Lateral view of rhinarium of *Bassaricyon* sp.?
E. Ear of *Bassaricyon alleni*. (Sketched without measurement from dried skin.)

a semicircular flap of integument rising behind the adjacent free edge of the pinna, its anterior rim being deeply emarginate. Judging from dried skins, the bursa of *Jentinkia* is similar to that of *Bassariscus*. I also find it present in dried skins of *Bassaricyon*, but it appears to be less well developed than in *Bassariscus*. The upper portion of the posterior flap arises behind the margin of the pinna, but its lower portion is confluent with it, and its anterior rim is lower and apparently not emarginate. The only other genus in which it is present is *Nasua*, where it has the form of a shallow pouch near the edge of the pinna which bulges slightly at this point. A similar bulge on the ear may be seen in *Procyon*, but in no example examined was there a trace of the pouch, and there is no trace of it in *Potos* or *Ailurus*. There is also no trace of it visible in the mounted example of *Ailuropoda* in the Natural History Museum, and it is absent in all the genera of Ursidæ.

If, as I believe, a well-developed *bursa*, such as is seen in the Felidæ and Canidæ, is a primitive feature in the Carnivora—and its presence in some of the genera of all the recognised families, except the Ursidæ, suggests that conclusion,—it follows that the ear of *Bassariscus* is the most primitive type in the Procyonidæ. Next comes that of *Bassaricyon*, then of *Nasua* showing stages in its suppression which has been achieved in *Procyon*, *Potos*, and *Ailurus*.

The following table summarises the characters of the ears in the genera examined :—

a. Bursa retained.
  b. Bursa marginal, at least the upper end of the posterior flap attached behind the adjoining edge of the pinna.
    c. Lower end of posterior flap behind the edge of the pinna; anterior flap emarginate; ears large ..... *Bassariscus, Jentinkia.*
    c'. Lower end of posterior flap confluent with edge of pinna; anterior flap with low straight edge; ears small ..... *Bassaricyon.*
  b'. Bursa a shallow pouch in front of posterior edge of pinna.. *Nasua.*
a'. Bursa suppressed.
  d. Ears large, expanded, and more or less pointed ..... *Procyon, Ailurus.*
  d'. Ears small and rounded ..... *Potos.*

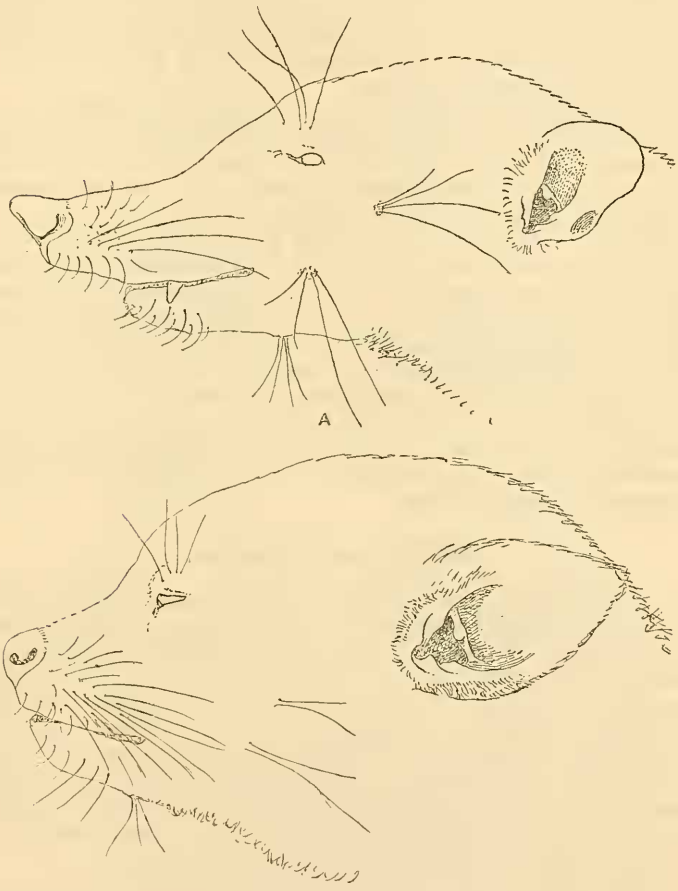
By this table *Ailuropoda* would fall alongside *Potos* under the heading *d'*. In the Ursidæ also no trace of the bursa remains and the ears are always rounded. They may, however, be comparatively large and rounded as in *Selenarctos* * *tibetanus*, or small as in *Helarctos malayanus*.

* Mr. A. de Carl Sowerby has pointed out to me that Heude applied this generic name to this Oriental bear in 1901 (Mém. Hist. Nat. Chinois, v. pt. 1, p. 2). The later name *Arcticonus*, which I gave to it in 1917 (Ann. Mag. Nat. Hist. (8) xx. p. 129), lapses, therefore, as a synonym of *Selenarctos*. My excuse for missing this point is that the then recorder of the Mammalia in the 'Zoological Record' purposely refrained from quoting Heude's work on account of its general worthlessness in his opinion.

Facial Vibrissæ.

Mivart described the facial vibrissæ of *Procyon* as follows :— "The whiskers on each side have 5 or 6 bristles grouped together, and there are four sets of such groups. There is also a tuft over the eye, one behind the angle of the jaw, and one under the

Text-figure 2.



A. Head of *Nasua nasua*. ♂ ad. × ½.
B. „ *Ailurus fulgens*. ♂ ad. × ½.

middle of the chin." That is quite true ; but, in addition, the superior genal tuft is also present, although sometimes it is hard to detect when the normal tuft is reduced to a single vibrissa on

each side. Submental vibrissæ are also present. In this genus, therefore, the tufts of facial vibrissæ are normal for the Carnivora, consisting of mystacials, superciliaries, two tufts of genals, the lower behind the angle of the mouth, the upper below and behind the angle of the eye, submentals, and an unpaired interramal tuft.

I have no notes or sketches of the facial vibrissæ of *Bassaricyon*, but from Beddard's remark that there are five or six long vibrissæ forming the whiskers, three or four upon each cheek and two or three under the chin, I think it may be inferred that this genus falls into line with *Procyon* and *Potos* in having these tactile hairs normally developed.

In *Ailurus* the tufts of vibrissæ are also normal in number and distribution, and the upper genal tuft, represented by one or two vibrissæ, is situated low down on the cheek, only a little above the lower, and is often difficult to detect amongst the normal hairs which thickly clothe this portion of the head.

Similar tufts are present in the genera *Nasua*, *Bassariscus*, and *Potos*, being better developed and consisting of stouter vibrissæ in *Nasua* than in the others. In two examples of *Potos* the upper and lower genals are represented by a single vibrissa each. In *Bassariscus* the upper genal tuft is set high up rather close to the angle of the eye, as is usual in predatory Mustelidæ. In *Potos* and *Nasua* it is lower down the cheek.

In *Ailuropoda* the mystacial vibrissæ are all short and obviously of little import as in the Ursidæ. On the single stuffed specimen examined I was unable to satisfy myself as to the presence of the other tufts.

The Muzzle and Rhinarium.

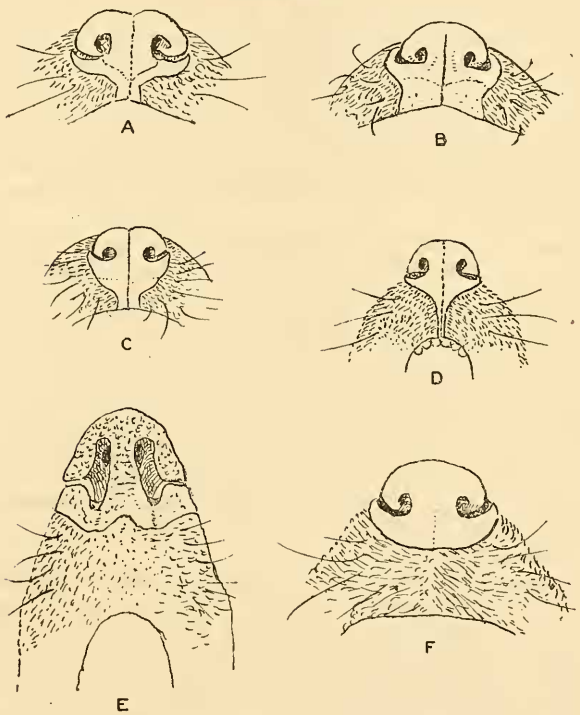
In *Procyon* the snout is moderately lengthened, and projects considerably beyond the lower jaw. The *rhinarium* is large and naked above. In front it has no central groove or, at most, a short indistinct one below. The upper margin is flat or evenly convex, not biconvex, and the width is much greater than the depth, but less than the combined depth of the rhinarium and of the upper lip. There is no trace of a philtrum, the upper lip being continuously, although comparatively scantily, hairy across the middle line, and the inferior edge of the rhinarium transverse in the middle and upcurled laterally. The internarial septum is broad and the infranarial portions moderately deep.

In *Bassariscus astutus* the muzzle is almost as elongated as in *Procyon*, the width of the rhinarium being much less than the combined heights of the rhinarium and of the upper lip; but the lip is cleft by a long narrow philtrum. The rhinarium itself is very like that of some Felidæ and Viverridæ, its upper edge being horizontal, with rounded angles from the anterior aspect and its inferior edge strongly angled mesially, where it passes into the philtrum. The internarial septum is moderately wide and

the infranarial portion comparatively shallow. There is a faint median groove marking the rhinarium from its summit to the bottom of the philtrum.

In *Nasua* the snout is much more elongated and mobile than in *Procyon*, and, as in that genus, the upper lip is entire, the rhinarium showing no trace of philtrum. The rhinarium differs from that of the other genera in certain particulars. Its upper anterior

Text-figure 3.



A. Rhinarium of *Ailurus fulgens*; front view.
B. „ *Potos caudivolvulus*; front view.
C. „ *Bassaricyon* sp. ?; front view.
D. „ *Bassariscus astutus*; front view.
E. „ *Nasua nasua*; front view.
F. „ *Procyon lotor*; front view.

All figures × ⅓ approx.

(D, E, F. Drawn with upper lip in same plane as anterior surface of rhinarium.)

margin is strongly produced. Its greatest width in front across the infranarial portions is less than the combined heights of the rhinarium and of the upper lip. The inferior edge is commonly strongly sinuous, owing to the median emargination. The nostrils

instead of being subcircular are markedly elongated from above downwards, and the internarial septum is long and narrow. The infranarial portions are deep, and are defined by a groove from the adjoining central portion, which has no trace of median groove.

To Beddard's description of the rhinarium of *Bassaricyon* as naked and marked with a median groove which also cleaves the upper lip and is visible on the dorsal side, I may add that in the specimen examined by me, the upper edge, when seen from the front, was lightly biconvex, the median groove was well marked and complete, the philtrum was short but barely as wide as the internarial septum, and that the infranarial portion on each side was exceedingly deep and marked with a faint transverse groove, meeting its fellow of the opposite side in the middle line; and that the total width of the rhinarium exceeded the height from the edge of the upper lip to the summit, the snout being short as in *Potos*, and not produced as in *Bassariscus* and *Procyon*.

In *Potos* the snout is not produced or slender, and the rhinarium is remarkable for the great width of the philtrum, which is as wide as or wider than the internarial septum, its sides often diverging below, and the greatest width of the rhinarium exceeds its height from the summit to the edge of the upper lip. The upper edge, seen from the front, is convex or lightly biconvex, the internarial septum is wide, the infranarial portions are very deep, gradually narrowing beneath the slit-like portions of the nostrils laterally. There is a well-marked median groove running from the edge of the lip and sometimes extending on to the upper surface in front, and a faint subhorizontal groove runs inwards beneath the nostril to meet its fellow of the opposite side in the middle line.

In *Ailurus* the snout is not produced, and the upper lip is divided by a short narrow philtrum, much narrower than the internarial septum, and the greatest width of the rhinarium considerably exceeds its height from the summit to the edge of the upper lip. The upper edge is tolerably evenly convex or markedly biconvex, the internarial septum is wide, and the infranarial portions are comparatively shallow, each being marked by a faint groove which extends obliquely downwards and inwards to meet its fellow of the opposite side in the middle line. The median groove is well marked, and extends from the edge of the upper lip often on to the summit of the rhinarium.

So far as it is possible to judge from the mounted specimen of *Ailuropoda*, the rhinarium resembles that of *Ailurus* in all respects, especially in the shortness and narrowness of the philtrum, except that its upper surface is entirely covered with hair. In this respect it differs from that of all the genera of so-called Procyonidæ and Ursidæ.

I was unable to satisfy myself as to the protrusibility of the lips in *Ailuropoda*, although the lower lip, as mounted, is slightly

compressed and pouted in the middle line. The point is not without importance, because all the Ursidæ differ from all the Procyonidæ and from *Ailurus* in having the lips protrusible or capable of being pouted. In the Procyonidæ and *Ailurus* the lips above and below the incisor teeth are comparatively closely adherent to the gums as in normal Carnivora.

By the characters supplied by the snout and rhinarium the genera may be classified as follows:—

a. Snout greatly elongated; upper edge of rhinarium produced beyond the nostrils so that its anterior surface is nearly flat and slopes obliquely downwards and backwards; anterior portion of nostrils vertically elongated, separated by a high, narrow, ungrooved septum, and almost concealed in profile view. Upper lip long and undivided by philtrum ..... *Nasua*.

a'. Snout not, or only moderately elongated; upper edge of rhinarium not produced, its anterior surface lightly convex, not noticeably receding; anterior portion of nostrils subcircular, separated by a low, broad, generally grooved septum, and visible in profile view.

b. Snout moderately produced; upper lip long so that the width of the rhinarium is less than the combined heights of the rhinarium and upper lip; median groove on rhinarium weak, or indistinct.

c. Upper lip undivided by philtrum; infranarial portion of rhinarium deep and wide, median groove abbreviated or indistinct ..... *Procyon*.

c'. Upper lip divided by long, narrow, groove-like philtrum; infranarial portion of rhinarium shallow and narrow, median groove complete ..... *Bassariscus*.

b'. Snout not produced; upper lip short, width of rhinarium exceeding its height from the summit in front to edge of upper lip; median groove strong.

d. Infranarial portion of rhinarium very deep.

e. Philtrum moderately broad ..... *Bassaricyon*.

e'. Philtrum very broad ..... *Potos*.

d'. Infranarial portion of rhinarium comparatively shallow and philtrum narrow ..... *Ailurus*.

By this key *Ailuropoda*, so far as it is possible to judge, would fall under heading *d'* alongside *Ailurus*, from which it differs in having the upper surface of the rhinarium covered with hair. The rhinarium is variable in the Ursidæ, being comparatively highly specialised in *Melursus* (Ann. Mag. Nat. Hist. (9) i. pp. 378–379, 1918).

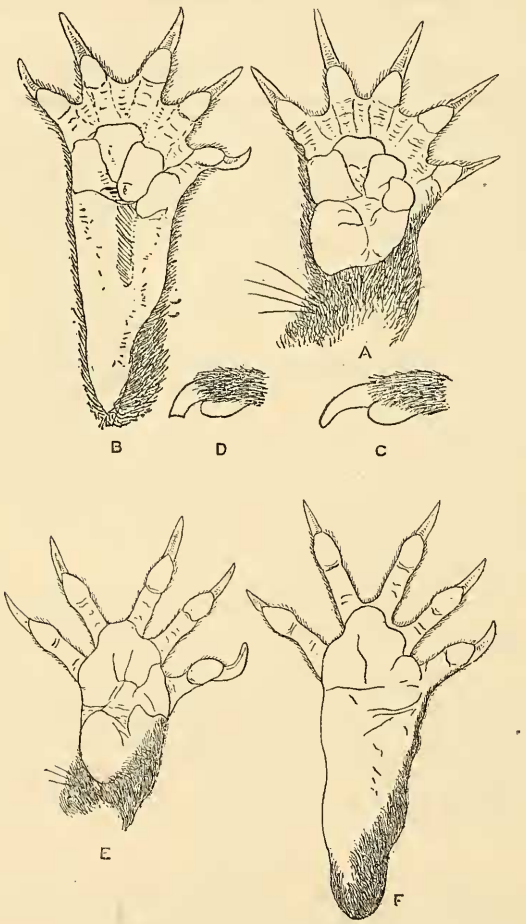
The Feet.

In describing the feet of the American genera, those of *Nasua* may be taken as a standard for comparison.

The claws of the fore foot are long, powerful, blunt and not greatly curved, and the digits are united by web, as described by Mivart, up to the proximal end of the digital pads. The underside of the digits and of the webs is entirely naked. The plantar pad is broad, moderately well defined and four-lobed. The two conjoined carpal pads, of which the outer is about twice as large as the inner, are together as wide as the plantar pad and

approximately equal to it in area. They are respectively in contact with the inner and outer lobes of the plantar pad; but in the middle line they are separated from it by a depressed area of smooth wrinkled integument. Above the carpal pad on the

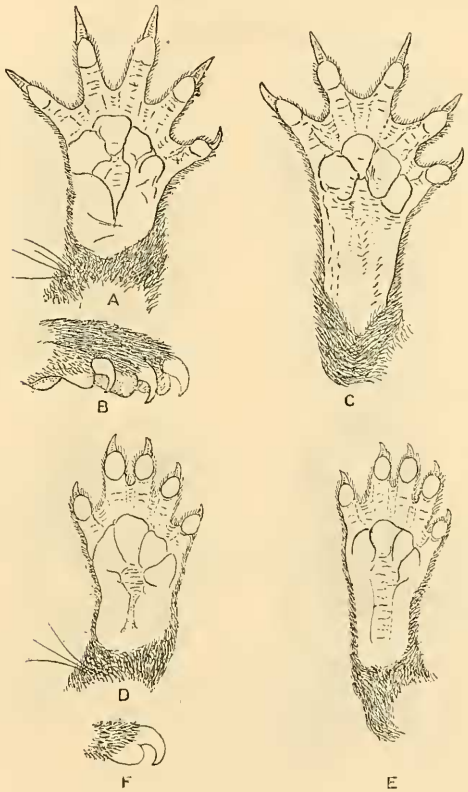
Text-figure 4.



A. Right fore foot of *Nasua nasua*.
B. „ hind foot of same.
C. Claw of fore foot.
D. „ hind foot.
E. Right fore foot of *Procyon lotor*.
F. „ hind foot of same.
× ½.

ulnar side there is a tuft of carpal vibrissæ. The claws and digits of the hind foot resemble those of the fore foot, except that the claws are somewhat shorter. The plantar pad is four-lobed; and above it the whole of the tarso-metatarsal area is

Text-figure 5.



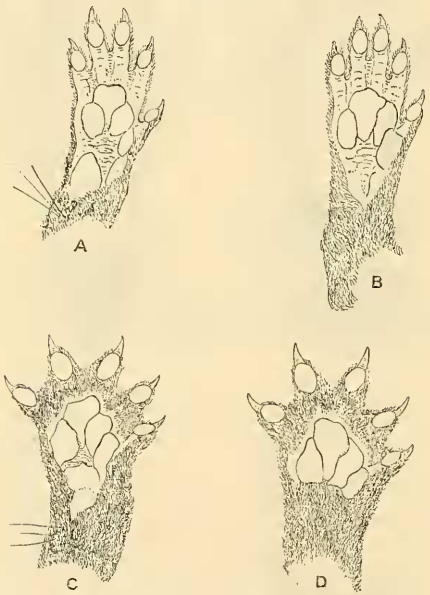
A. Right fore foot of *Potos*.
B. „ hind foot of same.
C. Claws and toes of fore foot of same.
D. Right fore foot of *Bassaricyon* sp.; digits not spread.
E. „ hind foot of same.
F. Claw of fore foot of same.
× ½.

naked as far back as the tip of the calcaneum, although the proximal third of the naked area is considerably narrower than the distal two-thirds. There are no definite metatarsal pads.

The feet of *Procyon* are a little less robust than those of

Nasua, the pads are less well defined and the claws rather smaller; but the great and essential difference lies in the complete absence of interdigital webbing, the digits being entirely free as far back as the plantar pads. This very rare phenomenon in the Carnivora is paralleled only, so far as I know, in the Crab-eating Mongoose *Atilax*, and in both cases it is probably subservient to delicacy of touch in finding and handling food.

Text-figure 6.



A. Right fore foot of *Jentinkia sumichrasti*.
B. „ hind foot of same.
C. „ fore foot of *Bassariscus astutus*; immat.
D. „ hind foot of same.

(A, B. Sketched from dried skin.)

× ½.

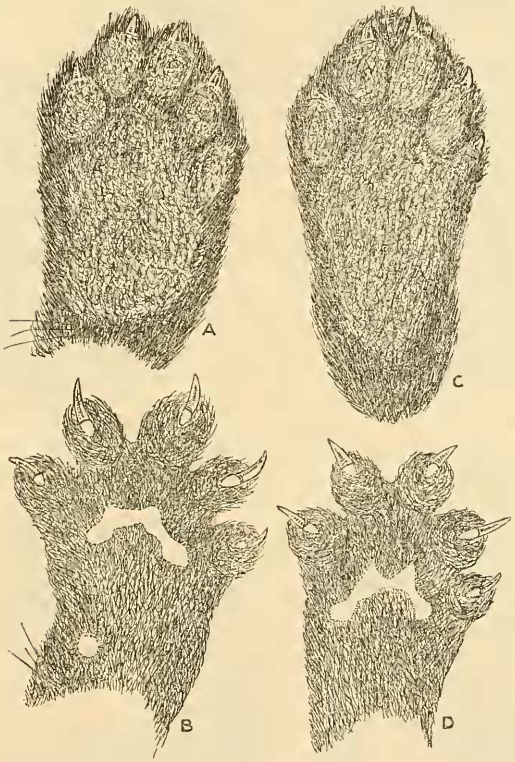
The feet of *Potos* * differ from those of *Nasua* in that the claws are shorter, sharper, and more curved; approximately the distal two-thirds of the digits are free from webbing, and, in the hind foot, the lower side of the calcaneum is covered with hair, the hair-covered area corresponding to the narrow naked area in *Nasua*.

* The feet of *Potos* were figured by Kidd to illustrate the development of the sensory ridges on the pads. The feet from which these figures were taken closely resemble those examined by me, but the metatarsal pads seem to have been better developed ('The Sense of Touch in Mammals and Birds,' pp. 24–25, figs. 9 & 10, 1907).

In *Bassaricyon* * the feet closely resemble those of *Potos*, the calcaneum being hairy beneath; but the interdigital webs are nearly as well developed as in *Nasua*. The claws are comparatively short and strongly curved and unlike those of *Nasua*.

In *Jentinkia sumichrasti*† the feet are seemingly very like those of *Bassaricyon* in the extent of the interdigital webbing

Text-figure 7.



A. Right fore foot of *Ailurus fulgens*.
B. The same with hair cut short and digits spread.
C. Right hind foot of same.
D. The same with hair cut short and digits spread.
× ½.

and the length and curvature of the claws, but possibly they are somewhat narrower. The great difference lies in the lower

* Beddard's figure of the fore foot of this genus showing the presence of the carpal vibrissæ agrees closely with my figure of this foot in the example I examined and sketched (see Proc. Zool. Soc. 1900, p. 663).

† I have unfortunately only seen of this species dried skins with the feet shrivelled or stretched. The main features of the pads were discernible, but I could not assure myself of the constancy in shape and size of the naked metatarsal area.

surface of the metatarsus, which is for the most part covered with hair, except for a relatively short, naked, proximally narrowed area just above the plantar pad. In this respect the feet of *Jentinkia* differ from those of the above-mentioned genera.

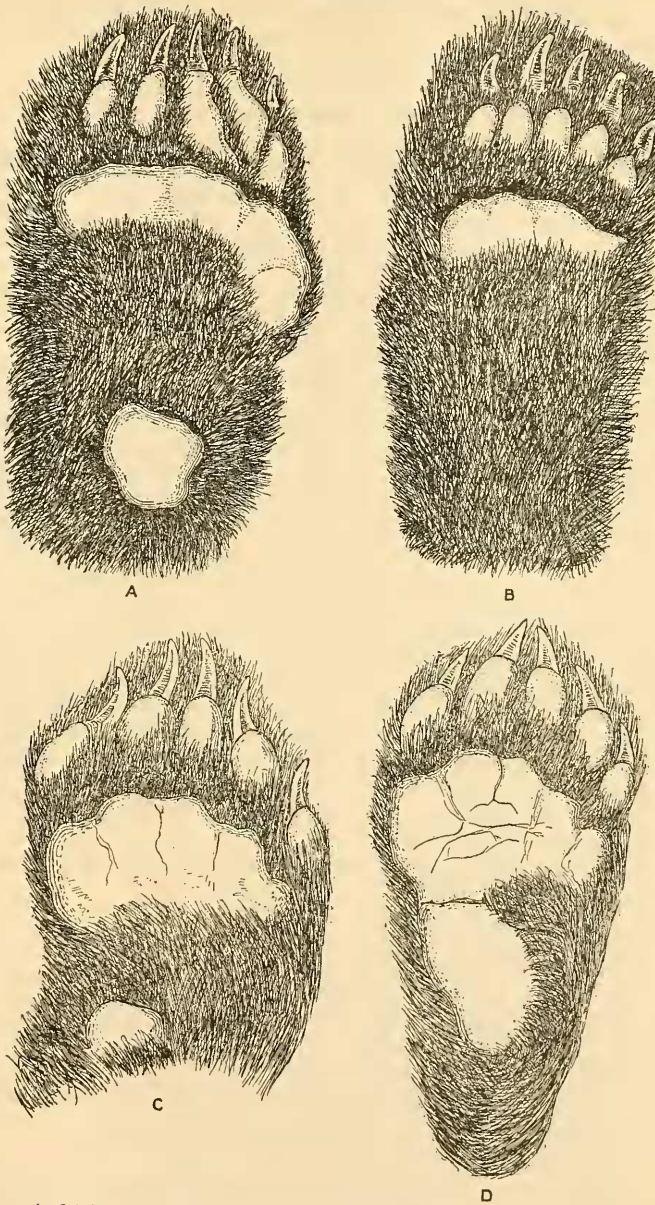
In *Bassariscus astutus* the feet are short, compact, and somewhat like those of *Genetta*, with short, curved, sharp claws and interdigital webs extending nearly up to the digital pads. They differ from those of all the genera previously described in having the lower side of the digits and of the webs covered with short hair almost as far back as the plantar pads, which are thick and strongly lobed. Also in the fore foot there is a single submedian carpal pad, which is elongated and narrowed proximally and much narrower at its distal end than the plantar pad, with which it is almost in contact. Furthermore, in the hind foot, the metatarsal area is covered with hair right down to the plantar pad.

It is mainly on the strength of the differences observed between the feet of *Bassariscus astutus* and of *Jentinkia sumichrasti*, which by most authors is referred to the genus *Bassariscus*, that I have preserved the genus *Jentinkia*. It is necessary to repeat, however, that I have only seen dried skins of *J. sumichrasti* and only one spirit-preserved example of *B. astutus*. Feet of dried skins of the latter seem, however, to agree with those of that example; but admittedly more material is required.

The feet of *Ailurus* differ from those of the American genera in the complete concealment of all the pads beneath the clothing of long and thick hair which everywhere covers the soles and in the consequent reduction of the pads to apparently functionless vestiges. Separation of the hair reveals vestiges of the pads as areas of naked, somewhat thickened skin, those on the digits being small subtriangular patches behind the base of the claws. The carpal pad is represented by a small subcircular patch remote from the plantar pad; but there is no trace of metatarsal pads. The plantar pads are reduced to transverse recurved areas, expanded at each end towards the base of the first and fifth digits and sending forwards two angular processes, longer on the hind than on the fore foot, approximately in line with the third and fourth digits. A further difference between these pads is that the inner (preaxial) arm is longer than the outer (postaxial) on the fore foot, the converse obtaining on the hind foot. The digits are united by webbing to approximately the same extent as in *Bassariscus*, and the claws are short, curved, and very sharp *.

* This description of the feet agrees in a general way with that published by Flower (P. Z. S. 1869, p. 754). He does not, however, mention the carpal pad, and describes the plantar pad as a "larger, transversely oval, bare space ·4″ [less than half an inch] across covered by pink soft skin." I assume that he did not trace the details of these pads to their full extent. Mivart would never have described the claws of the Panda as "blunt" if he had ever been scratched by them. The hairs on the soles of the foot of the Panda are a great disadvantage in climbing smooth branches. It is only with considerable difficulty that the animal can slowly ascend a stout branch, stripped of its bark, even when inclined at an angle of 45 degrees. It does so by means of the penetrating power of the sharp claws. It is not easy to suggest a meaning for the hairiness of the feet, since the animal does not live in a region of perennial snow. Possibly, however, it is to obviate slipping on wet branches.

Text-figure 8.



A. Right fore foot of *Ailuropoda melanoleuca*.
B. „ hind foot of same. (Copied from Milne Edwards's figure.)
C. „ fore foot of *Euarctos americanus*.
D. „ hind foot of same.

From the above-given description it is clear that the feet of *Ailurus* differ very materially from those of all the American genera, to which it is supposed by some authors to be tolerably closely allied.

The feet of *Ailuropoda* differ from those of *Ailurus* and of the American genera in being essentially Ursine in three particulars:—(1) The fore and hind feet are approximately equal in length, owing to the shortening of the hind; (2) the five naked digital pads form a slightly curved transverse line, the second and fifth lying respectively alongside the third and fourth, and the first (pollical and hallucal) touching the second when the digits are in contact; (3) the plantar pad is a wide naked transverse cushion, at least twice as wide as long and separated from the digital pads by a short area overgrown with hairs.

The fore foot further resembles that of *Ursus* and *Euarctos* in possessing a large carpal pad separated from the plantar pad by a long area overgrown with hair; but it differs from the fore foot of all the Ursidæ in the marked preaxial projection of the plantar pad beyond the line of the pollex. This gives additional width to the foot, and is doubtless correlated with the great development of the radio-carpal bone, described by Lankester, which simulates an additional metacarpal. The hind foot differs from that of the typical Ursidæ in that the entire sole is covered thickly with hair from the calcaneum to the plantar pad. It must be remembered, however, in this connection that in *Thalarctos* the corresponding portion of the foot is hairy, the metatarsal pad being reduced to a comparatively small lozenge-shaped area. The skeleton of the digits differs from that of the Ursidæ, as Lydekker pointed out, in the presence of a bony hood at the base of the terminal phalange. In the latter particular, as in the remoteness of the carpal pad from the plantar pad, the feet resemble those of *Ailurus*, but they differ therefrom in the large size and exposure of the pads and in the alignment of the extremities of the digits.

Excluding those of *Ailuropoda*, the characters of the feet may be summarized as follows:—

a. Soles of feet entirely and thickly covered with woolly hair concealing the pads, which are reduced in extent and thickness to apparently functionless areas of naked skin; carpal pad a minute naked area remote from the plantar pad ..... *Ailurus*.

a'. At least the digital, plantar, and carpal pads naked and well developed; carpal pad, or pads, comparatively large and in contact with the plantar pad, or nearly so.

b. Area between digital and plantar pads hairy; carpal pad single, much narrower than plantar pad; metatarsus covered with hair down to plantar pad ..... *Bassariscus*.

b'. Area between digital and carpal pads naked; carpal pads double, conjointly as wide as plantar pad; at least a small naked area on metatarsus above plantar pad.

c. Naked area of metatarsus reduced to a comparatively small patch, narrowing above ..... *Jentinkia*.

c'. Naked area of metatarsus extending over the greater part of that area.

d. Digits entirely free from webbing down to plantar pad ... *Procyon*.

d'. Digits united more or less by webbing beyond plantar pad.

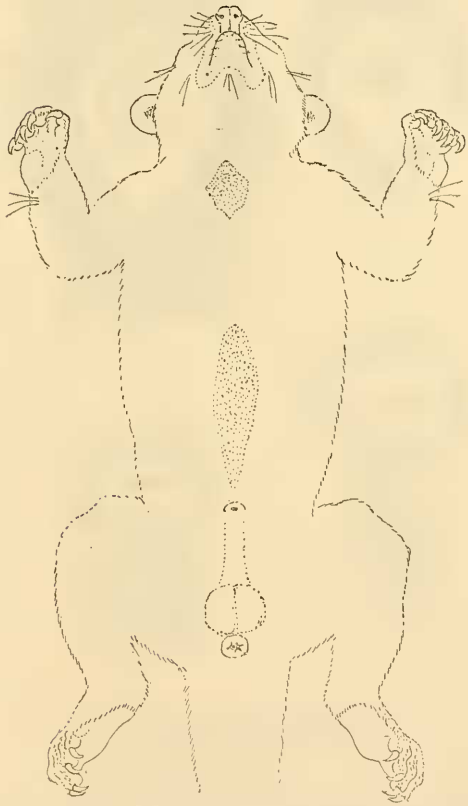
e. Claws fossorial, long, strong, and blunt; digits fully webbed up to digital pads; calcaneum naked mesially.. *Nasua*.

e'. Claws shorter, curved, and sharp; digits less fully webbed; calcaneum covered with hair.

f. Digits united by webbing for about two-thirds of their length ..... *Bassaricyon*.

f''. Digits united by webbing for about one-third of their length beyond plantar pad ..... *Potos*.

Text-figure 9.



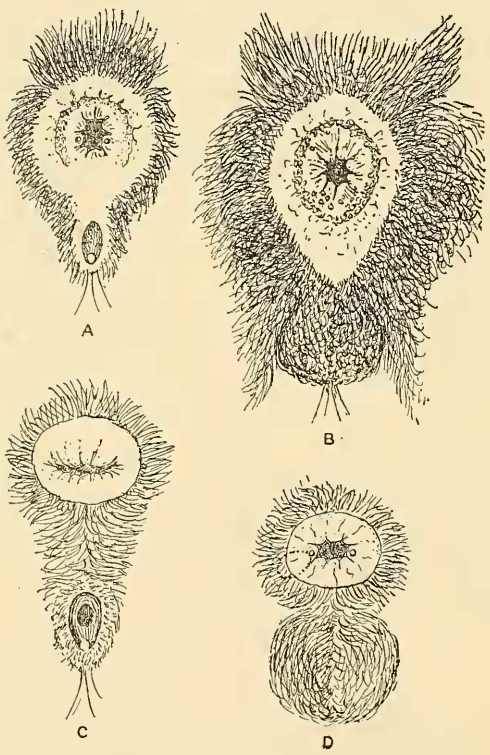
Ventral view of *Potos*, showing the median cutaneous glands, the position of the prepuce, etc.

Cutaneous and Anal Glands.

The only genus, known to me, which has specialized cutaneous glands, apart from those connected with the anus, is *Potos*. In

this genus there are two in the middle ventral line, one anterior and the other posterior. The former consists of a comparatively small patch of skin, scantily covered with short hairs and situated just in front of the anterior end of the sternum; and the latter, which is structurally similar to it, of an elongated tract on the abdomen, extending in the male from a point just in

Text-figure 10.



A. Anus and vulva of *Ailurus fulgens*.
B. „ scrotum of same.
C. „ vulva of *Procyon lotor*.
D. „ scrotum of same.

(In A and D the orifices of the anal glands are shown; in D the size and position of the gland of the left side is dotted in.)

front of the prepuce, where it is narrowed, over the umbilicus to the posterior end of the sternum. They are similarly placed and equally well developed in the female. These areas are not

sharply circumscribed at the margins, and the glandular portion is composed of well-developed normal skin-glands *.

Potos also has a considerable amount of nearly naked skin on the lower jaw and round the mouth. This, however, does not appear to be especially glandular. Probably the absence of the hair serves to keep the lips and chin clean from such sticky substances as honey, on which the Kinkajou feeds.

In *Procyon*, *Nasua*, and *Potos* the anus, like that of the Ursidæ, Canidæ, and others, opens in the centre of a circular, slightly protuberant area of naked skin, separated by hair from the scrotum or vulva. As Mivart stated, there is a pair of normal anal glands in *Procyon* like those of the Canidæ, but relatively a little smaller. Mivart also states that these glands are present in *Potos*; but I entirely failed to find even a trace of them in two examples, a male and female, the result of my examination confirming Owen's statement that they are absent (Proc. Zool. Soc. 1835, p. 122). Beddard does not appear to have looked for them in *Bassaricyon*. Their presence in *Bassariscus* was recorded by Gervais in the following passage (Voy. de la 'Bonite,' i. p. 19):—"Une petite plaque crypteuse circumanale existe à la terminaison de l'intestin, comme dans les Mangoustes, mais elle est moins grande que dans ces animaux et à sa surface débouchent de même les deux conduits des glandes anales." Although this passage suggests the presence in *Bassariscus* of a circumanal pouch like that of the Mongooses, I am disposed to think Gervais was merely describing the button-like area of naked skin immediately surrounding the anal orifice, such as is seen in *Procyon* or *Nasua*. This supposition is borne out by what he says as to the position of the orifices of the anal glands; and is further supported by the absence of a circumanal pouch in the male example of *Bassariscus* I examined.

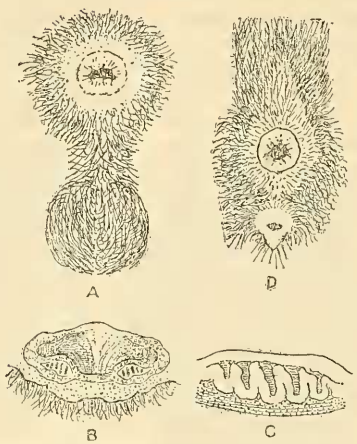
In *Nasua* anal glands are present, but in a much modified form, as Mivart pointed out. When the anus is opened, they appear as a series of four or five parallel slits, each series being set just within the orifice. The slits are the apertures of as many narrow sacs formed by the folding of the anal integument. These glands are quite different from those of any Carnivore known to me, and serve to differentiate *Nasua* tolerably sharply from its allies.

Flower described the anus of the male of *Ailurus*, pointing out the presence of a pair of normal anal glands and of a glandular area round the anal orifice. In the male I examined, the integument round the orifice corresponding to that seen in *Procyon*, for example, is highly glandular, and partially insunk so as to suggest the anal pouch of the Mungotidæ. Round it there is a considerable area of naked skin extending inferiorly to the

* These glands are conveniently placed for rubbing the secretion along the branches of trees to enable Kinkajous to track each other by scent. Although I have never noticed these animals behaving in a way to suggest that that is the function of the glands, I do not doubt that it is so.

scrotum, and from it the glandular central area is somewhat sharply marked off.

Text-figure 11.



A. Anus and scrotum of *Nasua nasua*.
B. Anus of *Nasua* opened to show the glands; the upper margin of the anus below.
C. One of the anal glands of *Nasua* in vertical section, showing the series of pouches opening upwards and the underlying muscle.
D. Anus and vulva of *Potos*.

The adult female possesses a similar glandular depression round the anus, but the surrounding area of naked skin is not so wide above and laterally, although extending inferiorly to the vulva *.

In an immature female, six months old, the anus is like that of *Procyon*, showing no special development of glands.

The four genera I have examined may be tabulated as follows by their specialized scent-glands :—

a. Anus opening in the centre of a shallow glandular pouch like that of the Mungotidæ; normal anal glands retained	*Ailurus*.
a'. Anus as in ordinary Carnivora †.	
b. Anal glands suppressed; two ventral cutaneous glandular areas	*Potos*.
b'. Anal glands retained; no ventral cutaneous glands.	
c. A pair of anal glands of the type normal in the Carnivora..	*Procyon* and *Bassariscus*.
c'. Anal glands peculiar, consisting of a series on each side of five shallow slit-like pouches	*Nasua*.

* Adults of both sexes of the Panda have the habit, so well known in the Mongooses, of rubbing the secretion of the anal region on the branches or other parts of their cage.

† On the assumption that my interpretation of Gervais' description of the anus of *Bassariscus* is correct.

Nothing is known of *Ailuropoda* with respect to specialized cutaneous or anal glands. The latter are probably present and the former absent. No specialized cutaneous glands have been discovered in the Ursidæ; but the anal glands are present or absent. Owen declared them to be absent, and I failed to find a trace of them in *Ursus arctos*, the type he probably examined. In an example of *Euarctos americanus*, however, I detected the normal pair, though relatively much reduced in size. The anus in this family resembles that of the typical Procyonidæ.

External Genitalia.

In *Procyon*, *Nasua*, *Potos*, and *Bassariscus*, and presumably in *Bassaricyon*, the prepuce is abdominal and far in front of the scrotum, as in the Canidæ, Ursidæ, and Mustelidæ, and the penis, which is supported by a long bone (*baculum*), is susceptible of protrusion from the preputial orifice for the entire length of the bone. The aperture of the urethra is on the ventral side of the bone in some vascular tissue which can be stretched to a certain extent beyond the apex of the bone.

In *Ailurus*, however, as recorded by Flower, the penis is comparatively quite short, the prepuce being close to the scrotum as in the Felidæ and Mungotidæ, although the penis is longer than in those families and structurally resembles that of the genera referred to the Procyonidæ.

Hodgson declared that *Ailurus* has no scrotum; and in the male examined by Flower that sac was represented by a pair of swellings between the anus and prepuce, the testes being internal. But in the male seen by me the testes had descended into the scrotum, which formed a quite distinct swelling below the anus, though not so constricted at the neck as in the examples of *Procyon*, *Nasua*, and *Potos* examined by me*.

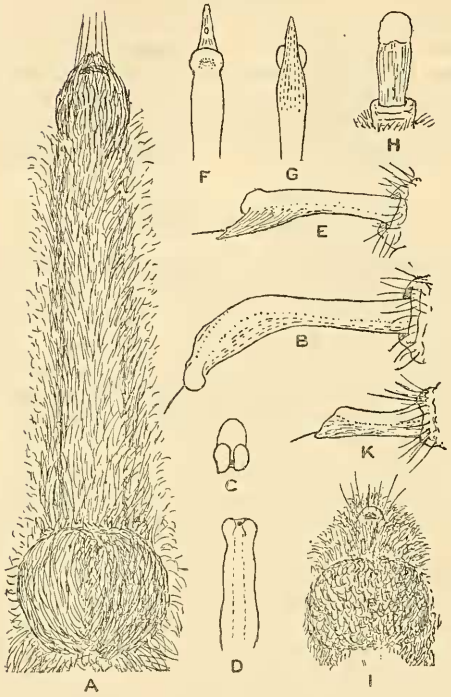
The baculum of *Procyon lotor* has long been known. It was figured by Blainville (Ost. des Mamm., Atlas i., *Subursus*, pl. viii.), and refigured and described by Gilbert (Morph. Jahrb. xviii. p. 818, pl. xxvii. fig. 8, 1892). It is relatively longer than in any other species referred to the Procyonidæ, surpassing 100 mm. along the upper curvature, the distal third of the bone being bent downwards. The apex is expanded both transversely and vertically, and forms a pair of condyle-like lobes separated by a deep notch.

According to Hollister, the baculum of *Procyon cancrivorus* (referred to the subgenus *Euprocyon*) is less curved than in the typical form, *P. lotor*; but the curvature is subject to a great deal of variation in the latter, *i. e.* from an angle of 135° to 90°.

In *Nasua* the baculum, as shown in Blainville's figure (*loc. cit.*),

* It may be added that Flower appeared to be quite unaware of the interest of the fact when he published the discovery of the proximity of the prepuce to the scrotum—a peculiarity in which *Ailurus* differs from all other Arctoid Carnivora.

Text-figure 12.



A. Ventral view of scrotum and prepuce of *Procyon lotor*, showing the abdominal position of the prepuce.

B. Lateral view of penis of same partially protruded from prepuce, with bristle thrust into urethral aperture; baculum dotted in.

C. Anterior view of extremity of penis of same, with urethral orifice between condyles of baculum.

D. Inferior view of distal portion of penis of same, showing course of urethral canal.

E. Lateral view of penis of *Nasua nasua* partially protruded; the slack ventral tissue pulled forwards and bristle thrust into urethral aperture.

F. Upper view of same.

G. Lower view of same.

H. „ „ penis of *Potos* partially protruded.

I. Ventral view of scrotum and prepuce of *Ailurus fulgens*, showing scrotal position of prepuce.

K. Lateral view of penis of same protruded almost to full extent, with bristle passed into urethral orifice with loose ventral tissue.

All figures except H × ½.

is straight or slightly curved and normally * subcylindrical and attenuated, with the apex expanded transversely and somewhat abruptly to a considerable extent. The sides of the expanded portion are rounded, and the distal margin is tolerably evenly truncated or mesially concave, so that the tip is slightly bilobate. The lower surface of the expanded termination is lightly convex; the upper to a corresponding degree concave.

In an adult male of each of the two species examined, namely *Nasua nasua* and *N. narica*, there is a difference in the length of the baculum. In the former species it measures 63 mm., in the latter 77 mm. Possibly this is a specific character †.

The baculum of *Nasuella* is, I believe, unknown.

The baculum of *Bassariscus* was figured by Blainville (Ost. des Mamm., Atlas i., *Mustela*, pl. x.), and described and figured by Gervais (Voy. de la 'Bonite,' i. p. 20, Atlas, pl. iv.). Disregarding the club-shaped base, it is tolerably evenly attenuated up to the apex, which has a simple undivided slightly depressed thickening, like the button on a foil. In the specimen figured by Blainville it was rather strongly upcurled in its basal third, with a slight downward distal curve, and measured about 50 mm. In Gervais' specimen it was straighter and measured the same, which, judging from the figure of the skeleton, was about two-thirds the basal length of the skull. In the young example of *Bassariscus* examined by me—an example in the stage of the tooth change, the milk premolars being still in place—the baculum, resembling in all essential particulars that figured by Gervais, is less than half the basal length of the skull, the latter being 65 mm. and the baculum 30 mm.

The baculum of *Jentinkia sumichrasti* as figured and described by Lönnberg (Anat. Anz. xxxviii. p. 232, fig. 2, 1911) measures 43 mm., is straight and subcylindrical, *i. e.* only gradually narrowed from the distal to the proximal end. The tip is a simple rounded condyle-like thickening; but close behind it, rather on the underside of the baculum, there is a pair of smaller rounded condyle-like tubercles, recalling the similar accessory processes in the baculum of *Potos*, which, however, project upwards and outwards.

As I have elsewhere remarked, the baculum of *Jentinkia* is very like that of the Musteline *Grison*, except that the post-apical processes in the latter are dorsal in direction. The presence of the two tubercles in question distinguishes the baculum of *Jentinkia* from that of *Bassariscus*.

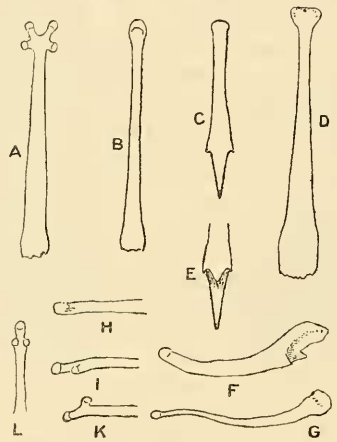
The only account of the *baculum* of *Bassaricyon* known to me is that of Hollister, who described it as "32 mm. in length,

* In one example of *Nasua nasua* the bone shows an abnormal flattening on the right side.

† In an adult but castrated male of *Nasua nasua* the baculum measures only 52 mm., and is exceedingly slender without any thickening at the proximal end. The penis was correspondingly short as compared with that organ in the entire male. One would perhaps expect the operation in question, if performed early in life, to affect the development of the baculum.

slightly bowed, and much less distinctly bilobed anteriorly than in *Procyon* or *Euprocyon*." I infer from this description that the baculum is of a simple type, resembling somewhat closely that of *Nasua*. I presume the bone was taken from an adult animal. If so, its small size as compared with that of *Potos* and the difference in the formation of the tip are interesting, although there is, of course, no reason to suppose that *Bassaricyon* is in any way nearly related to that genus despite their superficial resemblance in some particulars. In connection with the comparative shortness of the bone, it must be remembered that *Bassaricyon* is the smallest member of the so-called Procyonidæ.

Text-figure 13.



A. Upper side of baculum of *Potos*.
B. The same of *Bassariscus astutus* (immat.).
C. „ „ *Ailurus fulgens*.
D. „ „ *Nasua nasua*.
E. Proximal end of baculum of *Ailurus* from below.
F. Lateral view of baculum of the same.
G. „ „ „ *Bassariscus astutus* (after Blainville).
H. „ „ apex of baculum of *Nasua*.
I. The same of *Jentinkia* (after Lönnberg).
K. „ „ *Potos*.
L. Upper side of tip of baculum of *Jentinkia* (after Lönnberg).
Figs. A, D, H, K × ½ ; the rest natural size approximately.

In *Potos* the baculum is somewhat shorter than in *Nasua*, but, as in that genus, it is straight or slightly curved, subcylindrical, and attenuated. The apex differs from that of all the genera referred to the Procyonidæ. It ends in four condyle-like processes, one smaller, directed upwards and outwards on each side, and two at the end separated by a wide and deep notch. The two

bacula of this genus which I possess differ a little in length and in the development of the terminal processes. One measures 65 mm., the other 60 mm. The former is narrower at the base, but slightly thicker at the neck behind the two proximal processes, and these are smaller, a little less salient, and directed slightly less upwards. The baculum is wider across them than across the terminal processes, which project straight forwards and converge slightly at their inner angles, so that the notch between them is a nearly complete oval. In the shorter of the two the proximal processes are larger and the terminal processes diverge slightly from the middle line, so that the width across them is equal to the width across the proximal processes, and the notch between them is wider, and not narrower, at its mouth.

Flower figured and described the baculum of *Ailurus*. Conforming to the size of the penis, it is relatively very short, being only about an inch in length*. Its upper side is markedly concave, owing to the slightly upturned apex and the rather strongly elevated base. Its proximal half is flat below but compressed and carinate above. The tip is a little expanded and truncated, with rounded angles and only very obscurely bilobed, and there is a short median groove on the upper side just behind the tip. The epithet "spatulate" applied by Flower to the tip of the specimen he examined, does not express the shape of the termination of the bone in my example. This bone measures about 23 mm.

By the penis and baculum the genera may be distinguished as follows :—

a. Penis short, prepuce close to scrotum; baculum short, its apex simple and upturned, its base with a high keel ..... *Ailurus*.

a'. Penis long, prepuce abdominal; baculum long, not upcurled apically, its base clavate, not strongly keeled.

b. Baculum ending in four short, radiating condyle-like branches. *Potos*.

b'. Baculum ending otherwise.

c. Baculum curved downwards distally, its apex forming two rather deeply cleft condyle-like processes ..... *Procyon*.

c'. Baculum straight, or nearly so, distally, its apex at most indistinctly bifid.

d. Baculum with expanded, flattened, subspatulate, indistinctly bifid extremity ..... *Nasua* (and ? *Bassaricyon*).

d'. Baculum with rounded apex.

e. Two small condyle-like processes just behind the apex ... *Jentinkia*.

e'. No accessory processes behind apex ..... *Bassariscus*.

The length of the penis and the position of the prepuce, two very important points in the classification of the Carnivora, are unknown in *Ailuropoda*. The Ursidæ resemble the typical Procyonidæ in those characters; and in all the species I have examined the baculum is a long, stout, distally tapering bone, with a simple termination.

* That is to say about one-third of the length of the baculum in *Potos*, a smaller animal.

There is very little to say about the external genitalia of the female. In *Procyon* and *Ailurus* the vulva occupies the same relative position as in Canidæ and Ursidæ. In both genera it is an oval or egg-shaped excrescence, with hairy labia surrounding a central pit, the clitoris being a small excrescence near the lower edge of the pit, and above the clitoris is the orifice of the vagina. In *Ailurus* the clitoris contains a small bone; but I have no note of this in *Procyon*. In *Potos* the vulva is relatively a somewhat shorter angular prominence, with the orifice forming a transverse, not a vertical, rima—an adaptation possibly to the width of the tip of the baculum of the male. I found no clitoris within the orifice. Beddard did not describe the vulva in the female example of *Bassaricyon* he examined.

The External Characters as a Guide to Classification.

A review of the above-recorded characters brings to light some interesting facts bearing on the classification of the genera examined.

There is nothing special to say about the vibrissæ except their high development in *Nasua*.

The external ear shows in its variation generic features, but practically no evidence of close intergeneric kinship.

The muzzle and rhinarium also exhibit good generic characters; while the rhinarium of *Nasua* differs markedly in its specialization from that of the rest.

In the case of the feet, however, a marked difference may be noticed between *Ailurus* and the rest. In the latter a gradation may be traced from *Bassariscus* through *Jentinkia* to *Bassaricyon*, from the latter to *Nasua* on the one side and to *Potos* on the other, and from *Potos* to *Procyon*.

Ailurus also stands alone in possessing a specialized glandular area round the anus. The presence of normal anal glands both in *Ailurus* and *Procyon* merely indicates the mutual inheritance of a primitive feature; but the modification of these glands met with in *Nasua* is an acquired differentiating peculiarity, as also is their loss by *Potos*. The latter is also peculiar in the possession of the ventral glands.

Finally, *Ailurus* differs markedly from the rest of the genera in the scrotal position of the prepuce, the shortness of the penis and baculum, and the structure of the base of the baculum itself. The others retain the primitive abdominal position of the prepuce and the large baculum seen in typical Arctoids, all Cynoids, some Æluroids (e. g. *Cryptoprocta*), and the Pinnipedes.

The above-mentioned peculiarities of *Ailurus*, coupled with the better-known peculiarities of the skull and teeth, justify the severance of that genus from the American Procyonidæ as proposed by Gray and upheld by Gill, Turner, and Flower, though

subsequently abandoned by the latter and by most recent authors.

Potos, too, has several peculiarities in its external characters as well as in its skull and teeth; and probably no one will cavil at the adoption of Trouessart's view that it should stand as the representative of a special subfamily of Procyonidæ, namely Potosinæ.

The status of the remaining genera is not so easy to settle. Taking first the older known forms, *Procyon*, *Nasua*, and *Bassariscus*, there does not seem to be evidence of any close affinity between them, a fact clearly perceived by Gray and Gill, although by making *Nasua* and *Procyon* the types of special subfamilies of Procyonidæ, Gill expressed his idea of closer kinship between them than between either of them and *Bassariscus*, which he kept in a family apart. Even quite recently Hollister has adopted the view that *Bassariscus* should rank as a separate family.

The discovery of *Bassaricyon*, since the time of Gray and Gill, does not help matters, since the genus is equally isolated and serves in no respect to affiliate any two of the other three. The four genera, in fact, differ in a large number of characters, to any one of which full generic value would be granted nowadays; and the logical inference to be drawn from this argument is that the sum of the characters demands supergeneric recognition, which should be expressed systematically by elevating the genera to the rank of subfamilies. Further justification for this course may be found in following the present day tendency to grant full generic value to the characters upon which such forms as *Euprocyon*, *Nasuella*, and *Jentinkia* were founded. We shall then have the Procyoninæ, the Nasuinæ, and the Bassariscinæ with two genera each and the Bassaricyoninæ with one.

The Position of Ailuropoda.

The question of the systematic position of *Ailuropoda* cannot be passed by in a paper dealing with the Procyonidæ, since the genus has been referred to that family. Milne Edwards contented himself with pointing out the resemblances between *Ailuropoda* and *Ailurus* on the one hand, and *Ailuropoda* and the Ursidæ on the other. And, so far as I am aware, Mivart was the first author definitely to state the opinion that *Ailuropoda* is more nearly akin to the Procyonidæ, with which it is affiliated through *Ailurus*, than to the Ursidæ; and this opinion found practical expression in the ascription of *Ailuropoda* to the Procyonidæ, under a special subfamily also including *Ailurus*. Mivart's view was adopted, with the support of much additional evidence, by Lankester and Lydekker, and Mivart's classification was independently reached. Finally, Bardenfleth attempted to show that Flower was right in classifying *Ailuropoda* in the Ursidæ.

Bardenfleth appears to have been much influenced by Winge's opinion on the homologies of the cusps in *pm.* 4 of the upper jaw, which, admitting its correctness, shows that the structure of the tooth in question lessens the evidence for the affinity between *Ailuropoda* and *Ailurus* and strengthens the evidence for affinity between the former and the Ursidæ. The points are:—(1) The antero-internal cusp of *Ailurus* corresponds to the postero-internal cusp of *Ailuropoda*; (2) the postero-internal cusp of *Ailurus* is unrepresented in *Ailuropoda* and the antero-internal cusp of *Ailuropoda* is unrepresented in *Ailurus*; (3) the postero-internal cusp of *Ailuropoda* corresponds to the postero-internal cusp of the Ursidæ; (4) the antero-external and antero-internal cusps of *Ailuropoda* are unrepresented in the Ursidæ—in other words, *pm.* 4 of the maxilla of the Ursidæ corresponds to the posterior half of the same tooth in *Ailuropoda*, with the further difference that the inner and posterior roots of this tooth in the Ursidæ are, except in abnormal cases, fused. Nevertheless, the resemblances between this tooth in *Ailuropoda* and Ursidæ do not, in my opinion, justify the conclusion that *Ailuropoda* is a member of that family. For, if the tooth in *Ailuropoda* is not Ailurine or Procyonine, it is certainly not Ursine. It is peculiar and stands by itself, so far as living Carnivora are concerned.

Some of the characters cited as of systematic value by Lydekker and Bardenfleth are too inconstant to be of use. Steno's fissure, the cleft between the anterior palatine (incisive) foramina, is cited by Lydekker as diagnostic of the Procyoninæ, restricted to the American genera, which have it, and the Ailurinæ, including *Ailurus* and *Ailuropoda*, which are without it; and Bardenfleth states that it is present in *Ursus* and absent in *Ailurus* and *Ailuropoda*. The actual facts are as follows:—Even in the comparatively small series of skulls belonging to the Zoological Society, I find this fissure present in an example of *Ailurus*, where it is represented by a groove terminating in a foramen which passes up into the nasal passage—a condition which it commonly presents, even within the limits of the genus *Procyon*. As for the Ursidæ, it varies in size from a long cleft to a minute orifice, through which a needle-point can only just be passed.

Lydekker, endorsing Lankester's statement, also draws attention to the "important fact that *Ailurus* and *Ailuropoda* resemble the American Procyonidæ, and thereby differ from all other Carnivora, in the presence of two lobes or cusps on the inner or tubercular portion of the upper carnassial." Even if he had said "some of the American Procyonidæ," the statement would not have been true, because both *Helictis* and *Taxidea*, two of the Mustelidæ, have two cusps on the inner portion of the tooth. Again, "*Æluropus* approximates to the Racoon in the absence of postorbital processes of the frontals." This is not true, the frontal postorbital processes being well developed in all the skulls of

Procyon I possess*. Further on we read: "A point of resemblance between *Ursus*† and *Æluropus* is to be found in the circumstance that the maxillary [preorbital] foramen opens on the side of the skull well in advance of the zygomatic root, whereas in *Ælurus* and *Procyon* it perforates the zygoma itself." So far as this statement is applied to the Ursidæ, it is contradicted by the Malayan Bear, in which the foramen perforates the zygoma exactly as in *Ailurus* and all the American Procyonidæ. I may also add, in this short-headed species of Ursidæ the zygomatic width of the skull bears to the basal length about the same proportion as in *Ailuropoda*, thus contradicting Lankester's statement that "in all Bears the skull is much longer and narrower both in its facial and cranial regions than in the skull of *Æluropus*." Bardenfleth similarly wrongly contrasts *Æluropus* with *Ursus* when he says of the former "zygomatic arches exceedingly wide" and of the latter "zygomatic arches moderately wide"; and his statements that the basioccipital is broad and the bulla not inflated in *Ursus* are not always true of the species in question. These corrections, however, are of no great moment in settling the degree of kinship between the Ursidæ, *Ailuropoda*, and *Ailurus*—the point at issue between the authors quoted. What they prove is that the resemblances between the genera concerned are closer than either author claimed.

My own opinion about the matter is that Lankester and Lydekker, as Bardenfleth held, overrated the resemblances between *Ailuropoda* and *Ailurus* and underrated the differences; and that Bardenfleth underrated the peculiarities of *Ailuropoda* which distinguish it from the Ursidæ. The attempt to place *Ailuropoda* in the Procyonidæ makes the definition of that family an impossibility. For example, every character used by Lydekker for defining that family has its exception. The same criticism cannot be advanced against its inclusion in the Ursidæ, because in one or two well-marked characters, like the structure of the feet, the length of the tail, and the presence of *m.* 3 in the mandible, *Ailuropoda* and the genera of Ursidæ resemble each other, and differ from *Ailurus* and the American genera assigned to the Procyonidæ. But since the assignment of *Ailuropoda* to the Ursidæ disturbs the homogeneity of that family, which already has some half-dozen well-defined genera, I prefer to regard *Ailuropoda* as the representative of a distinct family. The genus is neither Ursid nor Procyonid, but something distinct from both.

* Bardenfleth also is wrong in stating that *Melursus* is without frontal postorbital processes.

† Fig. 3, Pl. xix. of Lydekker's paper (Tr. Linn. Soc., Zool. vol. viii.) is part of the skull of an *Ursus*, not of a *Procyon* as labelled.

Dichotomous Classification of the Ursidæ, Ailuropoda, Ailurus, *and the Procyonidæ.*

Although this method of classifying animals has its disadvantages on account of its deceptive simplicity and its concealment of cross resemblances, it has the convenience, if not admittedly artificial, of presenting clearly the characters relied upon by the author and of expressing his views as to the kinship of the groups concerned.

a. Feet short and broad, digits subequal, their pads forming a lightly curved line in front of the broad plantar pad. Tail reduced to an anal operculum. *M.* 3 of mandible retained. Carotid foramen situated at posterior end of bulla, close to *foramen lacerum posticum*.

a'. Cheek teeth comparatively small, especially *pm.* 1–*pm.* 3, which are mostly unicuspid and one-rooted, but *pm.* 1 larger and more persistent than *pm.* 2; upper *pm.* 4 at most tricuspid, its inner root normally fused with the posterior root. Lower *pm.* 4 short, unicuspid. Zygoma arising approximately above the middle of *m.* 2, which is far in advance of the mesopterygoid fossa, the latter preceded by a long edentulous posterior palate. Alisphenoid canal present. External auditory meatus with its floor produced to reach approximately to end of thick mastoid process. Mandible not thickened on inner side of coronoid, which does not conceal *m.* 3 and is comparatively low and but little hooked; angular well developed, condyle and glenoid surface not abnormally wide. Fore foot without long radio-carpal sesamoid etc.*... URSIDÆ.

a^2. Cheek teeth excessively developed, except *pm.* 1 of upper jaw, which is minute in maxilla, and absent in mandible; *pm.* 2 of maxilla and *pm.* 2 and *pm.* 3 of mandible tricuspid; *pm.* 3 of maxilla sexcuspid; *pm.* 4 of same, with three large outer and two large inner cusps, its inner root not fused with posterior root; lower *pm.* 4 long, tricuspid. Zygoma arising approximately above middle of *m.* 1; posterior end of *m.* 2 reached or overlapped by anterior end of mesopterygoid fossa; no long edentulous posterior palate. Alisphenoid canal absent. External auditory meatus with its floor abbreviated and falling far short of long compressed mastoid. Mandible thickened on inner side of coronoid, which conceals *m.* 3 and is high and hooked; angular much reduced; condyle and glenoid surface abnormally wide. Fore foot with long radio-carpal sesamoid etc.* ..... AILUROPODIDÆ.

b. Feet comparatively long and slender†, digits unequal, with their pads arranged in a strongly curved line round the comparatively narrow plantar pad. Tail at least long enough to reach the ground. *M.* 3 of mandible suppressed. Carotid foramen on inner side of bulla well in advance of *foramen lacerum posticum*.

b'. Penis short, prepuce close to scrotum. Pads of feet reduced and functionless, completely concealed by woolly hair; carpal pad remote from plantar pad. Anus in centre of glandular depressed area. *Pm.* 2 and *pm.* 3 of maxilla large and three-rooted; *pm.* 3 quinquecuspid and closely resembling *pm.* 4. Alisphenoid canal present. *Foramen rotundum* minute, lying beneath *for. lac. ant.*, the two separated by a very thin plate of bone and sunk in a common pit; *foramen ovale* elongate. Anterior edge of coronoid inclined forwards ..... AILURIDÆ.

* For other skeletal characters distinguishing the Ursidæ and Ailuropodidæ, see the papers by Lankester, Lydekker, and Bardenfleth.

† It is hardly an exaggeration to say that there is no such thing as a plantigrade carnivore. They all run and walk on the digital and plantar pads, whether they are cats, dogs, bears, or badgers. Bears, when standing on their hind legs, and sometimes when walking, place the metatarsal pads on the ground; but generally these pads, like the carpal pads, are raised from the ground in ordinary progression. A naked metatarsal area does not indicate platigradism, as has been supposed.

b^2. Penis long, prepuce abdominal, remote from scrotum. Feet with digital and plantar pads normally developed and quite naked; carpal pad or pads also well developed and close to the plantar pad. No glandular area round anus. *Pm.* 2 and *pm.* 3 of maxilla comparatively small and one- or two-rooted*; *pm.* 3 unlike *pm.* 4, at most with one main cusp and three minute cusps. Alisphenoid canal absent. *Foramen rotundum* of normal size, well separated from the *for. lac. ant.* and not sunk in a common pit with it; *foramen ovale* rounded. Anterior edge of coronoid inclined backwards ..... PROCYONIDÆ.

c. Mandible very massive, the rami early fused by a long symphysis, the lower edge straight by the growth posteriorly of a large lamina, sometimes rounded, sometimes angled, beneath the angular process, which is reduced to a small excrescence beneath the condyle†; inner dentary foramen beneath base of anterior edge of coronoid. Palate parallel-sided, as wide in front as behind, depressed behind molars; paroccipitals and mastoids standing away from bulla, which has carotid foramen set forwards much nearer *for. lac. med.* than *for. lac. post.*; molars even when newly cut flat-crowned; *pm.* 1 absent above and below‡. Tail prehensile. Two ventral cutaneous glands Anal glands aborted ..... *Potosinæ.*

c'. Mandible slender, the rami separable and with normal symphysis, lower edge arched and inclining upwards without expansion towards angular process, which is well developed and close beneath the condyle; inner dentary foramen about midway between the condyle and the anterior margin of the coronoid. Palate with arcuate sides, wider behind than in front, not depressed behind molars; paroccipitals and mastoids arising close to the bullæ, which have the carotid foramen about equally distant from *for. lac. med.* and *for. lac. post.*, or nearer the latter. Molars cuspidate when newly cut; *pm.* 1 present. Tail not prehensile. No ventral glands. (Anal glands retained in *Bassariscus, Procyon* and *Nasua,* unrecorded in *Bassaricyon.*)

d. Mesopterygoid fossa long, extending to posterior molars; molars and premolars with pointed or blade-like cusps; canines rounded in section, not grooved and not mutually sharpened. Bursa of ear with anterior flap emarginate, posterior flap attached behind edge of pinna. Metatarsus with at most a small naked area above plantar pad; claws short, sharp, curved; digits fully webbed or nearly so. Facial portion of skull and zygoma as under *e*; hamular in front of foramen ovale; no supplementary foramen behind carotid ..... *Bassariscinæ* §.

d'. Mesopterygoid fossa short, separated from molars by a long posterior palate. Molars with subequal conical comparatively blunt cusps; canines grooved, mutually sharpened. Bursa absent or reduced, its anterior flap at most very low and not excised. Metatarsus naked beneath.

---

* Exceptionally in *Procyon*, *pm.* 3 is three-rooted.

† This at all events is, I believe, the correct interpretation of this region of the mandible.

‡ Huet figures a mandible with it present on the right side.

§ Hollister gave full family rank to this group, because "The Cacomistles (*Bassariscus*), while exhibiting many of the characters of the Procyonidæ, differs so greatly in the nature of all the teeth that it seems impossible to retain them in the family. The dog-like premolars and molars, the rounded canines, and the evident though small secondary lobes on the incisors . . . . . all show unmistakable characters of the teeth of the Canidæ." Nevertheless, by a series of comparatively simple changes, the teeth of *Bassariscus* can be derived from those of such a Procyonid as *Nasua*, for example, or *vice versa*, and the secondary grooves and lobes on the incisors are not always more marked in *Bassariscus* than they are in *Potos*, and the grooves are often traceable in other genera. The teeth of all the genera attest the extreme plasticity of those organs. (See above, p. 418.)

e. Skull with muzzle short, not compressed above, preorbital foramen close to anterior rim of orbit, which is above *pm*. 3 or *pm*. 4; inferior edge of anterior nares normally formed; canines only moderately sharp in front; posterior root of zygoma not abnormally expanded; typically no supplementary foramen on inner side of bulla between carotid and *foramen lacerum posticum*. Upper edge of rhinarium not produced, its anterior surface convex, with normal nostrils and wide septum.

f. Mastoid small, not bigger than paroccipital and hardly surpassing auditory orifice; carotid foramen not behind middle of bulla; *foramen ovale* well behind tip of hamular; ridges of posterior palate marginal. Claws short, sharp, much curved; digits webbed for two-thirds of their length. Snout not produced; upper lip divided by wide philtrum. Bursa retained and marginal ..... *Bassaricyoninæ*.

f'. Mastoid large, larger than paroccipital and projecting far beyond auditory orifice; carotid foramen behind middle of bulla; *foramen ovale* not behind tip of hamular; ridges invading lower surface of posterior palate. Claws longer, blunter, and less curved; digits entirely free from webbing. Snout produced, upper lip undivided, no philtrum. Two normal anal glands. Bursa absent ..... *Procyoninæ*.

e'. Skull with muzzle elongate and compressed above; preorbital foramen remote from orbit, the anterior rim of which is above *m'*; inferior edge of anterior nares thickened and produced; glenoid portion of zygoma much extended antero-posteriorly; a very distinct supplementary foramen between carotid and *foramen lacerum posticum*. Upper edge of rhinarium produced, its anterior surface nearly flat, with vertically elongated nostrils and narrow septum. Digits with powerful claws, fully webbed. Anal glands a series of small pockets on each side. Mastoid as under *f*; palate as under *f'*; position of carotid foramen and *f. ovale* intermediate. Bursa retained but not marginal ..... *Nasuinæ*.